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STUDIES ON THE MAINTENANCE OF ADULT SQUID (*LOLIGO PEALI*). II. EMPIRICAL EXTENSIONS [1]

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This study is a direct continuation of previous work on the maintenance of adult *Loligo pealei* (Summers and McMahon, 1974) which, in turn, benefited from a preliminary study (Summers and McMahon, 1970). The present study represents a second operational year of the facilities described in part I (Summers and McMahon, 1974); reference should be made to that paper for descriptions of the equipment and many experimental conditions. Reports on related studies appeared subsequent to planning for the present work (von Boletzky, von Boletzky, Frosch and Gatzi, 1971; LaRoe, 1971; Arnold, Singley and Williams-Arnold, 1972; Mikulich and Kozak, 1971). These were mostly concerned with squid rearing, though LaRoe (1971) reported on the rearing and maintenance of the loliginid squid, *Dorytheuthis* (= *Loligo*) *plei* and *Sepioteuthis sepioidea*. Appropriately, other studies utilized species more tractable to laboratory maintenance i.e., Sepiolinae (5 species, von Boletzky, *et al.*, 1971) and the sepiolid, *Euprymna scolopes* (Arnold, *et al.*, 1972) Mikulich and Kozak (1971) reported briefly on the maintenance of an oceanic squid, *Todarodes pacificus*.

Materials and Methods

Aquarium modifications

Previons experience indicated that squid were injured through collision with the aquarium walls and suggested that this might contribute to early mortality (Summers and McMahon, 1970 and 1974). A number of tank modifications were suggested by investigators at the Marine Biological Laboratory with the intent of minimizing damage resulting from these collisions; none of them had been critically tested and some were completely untried. In our observations, vertical tank walls were most in need of modification and we thought survival improvements might be made if the walls could be made both smooth and yielding. We had little information on optical properties of the wall which might reduce the numbers of collisions.

A bumper system was developed through trial construction which provided several desirable features; this is shown in Figure 1. It consisted of clear polyethylene tubing, $3\frac{1}{2}$ mils (0.90 mm) in thickness and 18 inches (46 cm) in flattened diameter hung vertically approximately 3 cm inside of the tank walls. The lower edge was held down by threading in two strands of lead-core line, the type used as a lead line for small seine nets. The top edge was alternatively taped to the flanged

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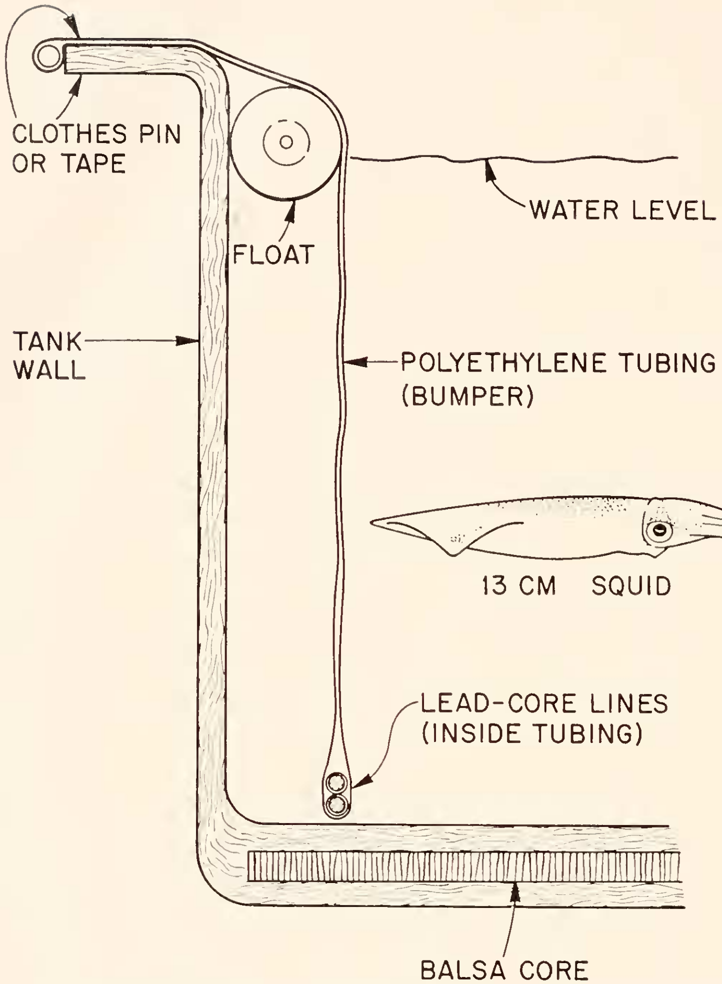

FIGURE 1. Typical cross-section of the bumper system at a tank wall. Squid colliding with the bumper must express seawater from the space between the polyethylene tubing the tank wall before striking a solid obstacle; this provides viscous damping of their kinetic energy. The bumper returns to its original position after a collision.

tank edge or clipped to it by threading a small polyethylene line through the tubing and attaching clothespins at close intervals. Adjustments were made at the tank flange to obtain a uniform, straight hanging surface all around the tank, and the ends of the tubing were overlapped with the inside lap folded back on itself. Spacing relative to the tank walls was accomplished by 13 × 3 cm hard plastic seine floats strung end to end on a small Nylon line at the water level between the wall and the polyethylene tubing. During the last three experiments, the bumper system was modified by eliminating tank corners. In this case, the upper edge of the polyethylene tubing was run at a 45° angle across each corner, thus excluding (in plan view) four isosceles triangles 30 cm on a side from the tank. The float line was shortened in this instance to take up slack tubing, effectively further rounding the corner.

The bumper system afforded tremendous viscous damping to any direct blow caused by squid and quickly returned to its original configuration after an impact. Water trapped behind the polyethylene tubing had to be forced out of a narrow space before the bumper would collapse; the more rapidly this was attempted, the more damping provided. Though hard, the floats were both light in weight and ellipsoidal, presenting little obstacle to a collision. The polyethylene tubing was visible in seawater and quickly acquired a noticeable microflora. When used simultaneously, bumpers were necessarily collapsed in the immediate vicinity of barriers.

Sources

Live squid were taken in the vicinity of Woods Hole, Massachusetts on eight separate occasions ranging in date from May 18 to November 10, 1971 (see Summers and McMahon, 1974). All but the third consecutive batch were trawled by the R/V CIONA, utilizing a 38–46 bar net (George W. Wilcox Company, Mystic, Connecticut). This otter trawl net was made from 15 thread Nylon netting material with a mesh size (stretched measure) of 10 cm. The cod end was lined with a knotted, soft-lay cotten netting material having a mesh size (stretched measure) of 3.5 cm. The trawl was fished from a single warp with 15 m legs, wooden doors (weighing 50 kg each) and a towing bridle 37 m long on each side of the towing swivel. A steel hoop between the cod end and liner prevented crushing of the catch, and the CIONA was especially rigged for quick emptying of the net into seawater-filled sorting tubs on the deck. Handling aboard ship and from dockside to the experimental tanks has been previously reported (Summers and McMahon, 1974).

The third batch of squid was taken in Great Harbor, Woods Hole, Massachusetts, adjacent to the National Marine Fisheries Service dock on the night of June 11–12, 1971. Lighting was rigged on the dock to attract prey animals; when the squid appeared, they were encircled with a 61 m (long) by 3.5 m (deep) seine net constructed of knotless Nylon netting with mesh sizes of 5 cm (stretched measure). Squid were bailed into a netting pound and transferred to the experimental tanks (the next morning) by the same method used for trawl-caught squid.

A total of 246 live squid were used in eight experiments (126 males, 106 females and 14 with no sex data). Age composition for the sexed squid was estimated from population studies (Summers, 1971) to be 10% young-of-the-year, 62% one year olds and 28% two year olds. One and two year olds were mixed in the four batches ranging in capture dates from May 18 to June 29, 1971. One year olds were mixed with young-of-the-year in the two batches caught on September 22 and November 19, 1971. Unmixed one year olds were taken in the two batches of August 4 and August 18, 1971.

Design

The experimental design called for an approach to the maximum possible squid survival through a series of internally sound experiments. Flexibility between individual experiments was to be exploited in order to attempt new innovations. At least one series of experiments was to be capable of determing the variability in survival within and between batches of squid. In contrast to the previous year's work (Summers and McMahon, 1974), a few obvious, though unproven, factors would be accepted as logical requirements. Thus, all squid were to be fed (on demand, to the level of two live *Fundulus* spp. per day) and crowding would not be used as a factor. Insofar as the supply of squid allowed, crowding was to be constant from experiment to experiment at numbers which assured good statistical evaluation. Relative water temperature was to be carefully studied, as was the shape and size of the maintenance tanks. The basic 2^n factorial experimental design was to be employed, examining several (n) factors at two levels each. Replicates were to be provided, and analysis was to be conducted by an analysis of variance (ANOVA) of individual experiments and of pooled data from suites of similar experiments. Pertinent data would be kept to provide a basis for the analysis of several conditions not employed as experimental factors.

Due to mechanical problems, seawater temperature control was not available during the first 2 experiments and the relative water temperature factors was not tested. Instead, a 2^2 factorial experimental design was employed which tested the factors bumpers and dividers (levels in both cases were with *vs.* without the particular devices). Because two basic tank shapes were used, this design provided tests of three experimental cell volumes (520, 1040 and 1560 liters) and five cell shapes (0.92×1.83, 0.92×3.66, 1.37×1.22, 1.37×2.44 and 1.37×3.66 m, all with water depths of 0.31 m). Crowding was held constant at three squid per 520 liter unit volume.

The third experiment had a 2^3 design; it was run as an incomplete block with the highest order interaction confounded with the two blocks. In other words, one-half of the experiment was run by sacrificing a test for the highest order interaction. Four tanks were used without dividers and the three factors were bumpers (levels: with *vs.* without), relative water temperature (ambient *vs.* chilled approximately 5° C below ambient) and tank levels (upper *vs.* lower). (With undivded tanks, the term "experimental cell" or simply "cell" is synonymous with "tank.") Squid for this one experiment had been caught in a seine and crowding was held at four squid per 520 liter unit volume.

The fourth through eighth experiments had a 2^2 design with factors tank levels and relative water temperature. Bumpers were used in all tanks and bumper corners were rounded in the last three experiments, as dscribed above. Crowding was maintained at three squid per 520 liter unit volume (30 squid in all) except in the fifth consecutive experiment, when fishing conditions had been poor and one less squid was used in each tank (for a total of 26 squid).

As in work of the previous year (Summers and McMahon, 1974), observations were made on an average of once every 9½ hours, and data logging was unchanged. Operational aspects of the experiments (*e.g.*, tank cleaning, physical conditions and randomization between experiments) was as previously reported. The principal statistic was the elapsed time at which an individual squid was found dead.

With minor exceptions, the facilities functioned without failure for the 179 days required to complete the eight experiments. Seawater flow stopped briefly once (September 28) with no apparent effect on the 16 squid then occupying the seventh experiment. In two experiments (the fourth and seventh), individual squid introduced a new problem by their prolonged survival. Because it was inefficient to commit the facilities indefinitely to single squid, these individuals were moved to another tank 16 and 8 days, respectively, after the death of the next longest lived batch-mates (surviving an additional 12 and 17 days, respectively). A standard Marine Biological Laboratory (fiberglass) sea table (of approximately 150-liter capacity) was the substitute tank and, excepting continuous illumination, no special attempt was made to duplicate experimental treatment combinations.

Results

Mean survival of all squid was 177 hours (approximately $7\frac{1}{3}$ days) and individual experiments had mean survival times ranging from 90 hours to 371 hours. Maximum survival of individual squid was 1124 and 1400 hours, for one year old, sexually mature female and male squid, respectively. No statistically significant results were detected in the first or second experiments testing bumpers and dividers (nor in pooled data from the two experiments), although there was an apparent direct correlation between survival and the absolute size of the experimental cell. In the third experiment, the survival advantage of the bumper system was demonstrated with better than 99% confidence of significance. In the last five experiments, tank level and the first order interaction of tank level and relative water temperature were found significant with better than 95% confidence in one experiment each. No significance was detected in the pooled data from this suite of five experiments, nor was there a signficant difference in the survival between *vs.* within batches. Although not statistically significant (except in one experiment), upper tanks regularly produced longer survival than lower tanks.

Minimum seawater temperatures were not artificially depressed below 8° C because earlier experience indicated that these were unnaturally cold for *L. pealei* (Summers, 1969; Summers and McMahon, 1974). Extreme range of seawater temperatures in the experiments was 8.6–10.0° C to 20.9–23.0° C. Relative water temperature was not found significant in any experiment or suite of experiments, nor was there a correlation found between absolute temperature and survival.

Discussion

No experiment during 1971 had a mean survival time as low as the mean of the previous year's results (87 hours). The probability of this occurrence in the same population is one in 256, suggesting that a distinct change was brought about in 1971. An apparent evolution in experimental design may be seen in the results. The first two experiments were run without temperature control and failed to show the value of the bumpers, but gave a mild indication of a correlation between absolute cell size and survival (a least-square fit of the data gives a 7% increase in survival time for each 520-liter unit volume increase in experimental cell). Thus, the third experiment with factors: bumpers, (undivided) tank levels and relative water temperature. Determination of high significance for the bumper system coupled with an estimated 90% significance for the bumper/divider interaction in the second experiment, suggested that the value of bumpers was less discernible in small cells. The final experimental design, then, incorporated bumpers while continuing to test relative water temperature and tank levels. Though no consistent significance was found among these factors in the last five experiments, a two-fold improvement in survival time was realized.

The mean survival times of the fourth through eighth experiments were: 205, 100, 371, 221 and 195 hours, respectively. As stated earlier, the fourth and seventh experiments benefited from one especially long-lived squid each (whose ultimate, although modified, survivals were 5–6 times longer than their respective batch means). The distribution of survival times for the sixth experiment was more uniform than for other experiments, but no observation concerning either the fishing conditions or the experiment itself suggest a cause for this result. (The first observation of mortality in this experiment occurred at 89 hours, the last at 719 hours.) On the other hand, the fifth experiment had a bad start on the fishing vessel. The trawl contents contained unually large numbers of Sea Robins (spiny) and skates (rough skinned). Though fishing had produced ample squid, few survived the journey to the experimental tanks and a reduced number was eventually employed. Compared with similar experiments, mortalities began to appear early, and continued at a high rate for about 100 hours; the last squid was found dead at 306 hours. In spite of contrasts between these five batches, the distribution of mortality was sufficiently broad to mask testable contrasts within *vs.* between them. Mean survival for the five experiments was 218 hours; it was 248 hours if the fifth experiment was thrown out and 262 hours in the last three experiments in which bumper corners were rounded. One-way analyses of variance between all possible pairs of experiments number four, six, seven and eight, were significant (with 95% confidence) only in the contrast between the last two.

The selection of squid for the survival experiments obviously affected the results. An increase in survival from year to year and within experiments conducted in 1971 may be due, in part, to improvements in capture techniques, handling and/or sorting before use. The significant test of the bumper system (in the third experiment) may have been enhanced by utilization of relatively undamaged, seine-caught squid. Poor results in the fifth experiment can probably be attributed to detrimental trawling conditions. Available data do not suggest unusual conditions in the exceptional sixth experiment.

As is the case with most attempts to maintain animals, we were aware of the fact that some squid were becoming "tame." This phenomenon was especially apparent in a pet squid given to us at the end of the summer (1970) by Dr. Ralph Hinegardner. This animal survived 28 days, the last six in our care. It would come to the surface of the tank when gently approached and take both live and killed food from the hand. This animal was a one year old female, and she deposited a number of egg masses in captivity, the last of which were infertile. The Hinegardner squid, like our longer-lived ones, did not so readily race around the tank as "wild" squid, though all of them could be startled. Our long-lived squid overcame transportation to new surroundings with less apparent trauma than most squid exhibit on first being placed in any tanks. All long-lived squid learned to take notice of our activities and seemed to recognize feeding times. No attempt was made to tame the experimental animals, though our observations cause us to suggest that it is possible, realizing that the squid may have the same object in mind.

Damage to the tail end of the captive squid was previously reported (Summers and McMahon, 1974). Bumpers reduced this damage, but introduced a new hazard, because squid would slip under the tubing, getting between it and the tank wall. (We restored all such errant squid to the tank center at each observation.) Though restrictive, this change in location was not usually fatal, and it appeared to us that some smaller squid (especially females) sought it out to avoid other squid. Careful adjustment of the bumper height helped prevent entrance to this narrow space, but no complete solution was found. Rounding of the bumper corners aggravated the problem of adjustment while preventing squid still inside the bumper from their senseless battering in corners. One of us (Ruppert), made preliminary tests on an alternative bumper or divider which was created by a continuous curtain of small air bubbles. Simple experiments in a tank generously provided by Mr. Charles L. Wheeler of the National Marine Fisheries Service (Woods Hole), demonstrated that squid usually would not cross such a barrier even if they were starved and live *Fundulus* (which also respected it) were on the other side. Although the technology of creating a uniform bubble curtain is complex, applications of this device might be suitable for squid maintenance facilities.

Mr. John Aldrich of the Boston University Marine Program (Woods Hole) kindly performed oxygen analyses of seawater in the experimental tanks. Samples were taken at six locations (the inlets to each upper tank and at the centers of the four experimental tanks) on four different dates (August 19 and 24, September 1 and 8, 1971). Seawater temperature ranges were 20.4–21.8° C in the ambient temperature tanks and 15.0–17.4° C in the chilled tanks. The total range of his 24 titration determinations was 4.31 to 5.25 ml of dissolved oxygen per liter, corrected to standard temperature and pressure; these values approach appropriate saturation levels. No consistent trend was measured in the water course of either tank stand, and no consistent difference was observed between stands; the maximum variation within readings from the same data and tank stand was about 0.5 ml/liter. The pH was determined at these same six locations on September 1 and 10, 1971. It was constant at all locations on each date; 8.05 on September 1 and 7.98 on September 10 (seawater temperatures of 15.6 and 21.0° C). No dissolved zinc analyses were made, because effects produced by the galvanized heat exchanger were confounded with relative water temperature, and the latter was not found to be a significant factor.

The apparent anomaly of longer squid survival in the most oblong tanks occurs in the present results as it did in the previous study (Summers and McMahon, 1974). Though not statistically significant in current results, survivorship was longer in the upper tanks. It may be noted that the "rectangular cells" in previous work were located in these same upper tanks because cell shapes were physically nested in tank levels. Without evidence for changes in water quality, we can only assume that these upper tanks are particularly suited for survival.

Squid survival was broken down into components by age, sex, and season because these three were interrelated. Results are graphically presented in Figure 2. Sizes of individuals in the different age groups (which were used in identifying the age groups) were practically the same as those reported for the previous year (Summers and McMahon, 1974). Seasonal occurrence of the age groups was slightly different due to the small sample sizes provided by these experimental animals. As previously observed, two year olds may hold a small survival advantage over one year olds when these are mixed together early in the season. Young-of-the-year squid show a great disadvantage in survival when mixed with one year olds. We also observed that young-of-the-year squid suffered more skin abrasions in the trawl than older age groups and that smaller squid receive a greater amount of abuse from their tank mates.

An apparent trend in survival of one year olds through the season probably reflects changes in experimental design, principally the removal of dividers and universal installation of bumpers, as well as the annual reduction in proportion of sex-

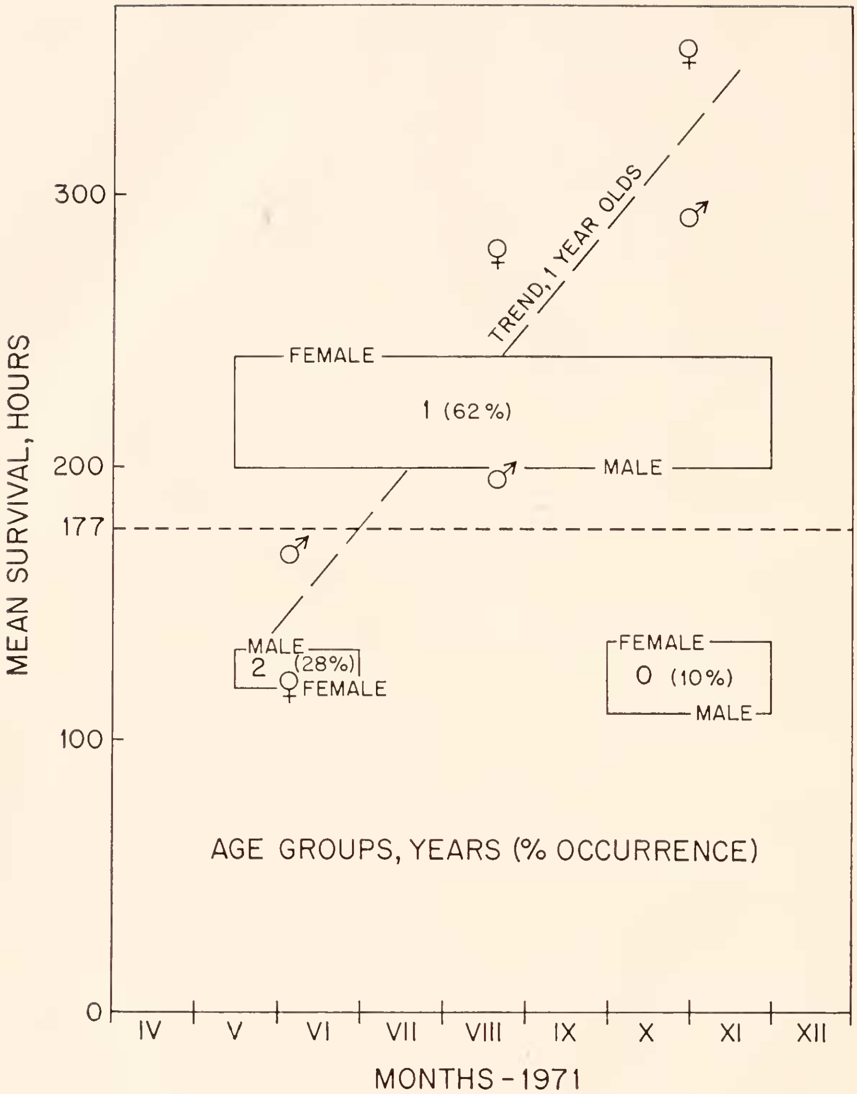

FIGURE 2. Mean survival of squid by age, sex and season. The overall mean, 177 hours, is indicated in the figure. Insets represent the seasonal occurrence of a particular age group in the experiments and the range of survival times for both sexes as designated on the boundaries. Data for one year olds has been broken down into three equal time periods as shown by paired sex symbols in the figure. An apparent trend in the survival of one year olds probably resulted from annual changes in sexual maturity and improvements in experimental technique.

ually mature squid. It is interesting to note that the initial survival advantage for breeding males gave way to a survival advantage for females later in the season, when sexual maturity, breeding and egg deposition were uncommon.

LaRoe (1971) reported maximum survival of *D. plei* of 38 days and maximum longevity of reared *S. sepioidea* of 146 days (the latter had attained a size of 10.5 cm). His conclusions were that both species of loliginids required 30–60% of their body weight in live food (mysids and larval fish) daily and would starve when fed less than 10–15% of their body weight. He favored opaque tanks (the largest of many different sizes were best), timed lighting which included ultra-violet wavelengths and "semi-natural" substrates in the tanks (sand, gravel, rocks and plastic grass). LaRoe kept adult squid in polyester resin impregnated, wooden tanks, of either 1900 or 2100 liter capacity; these had an exchange of filtered, running seawater once every 4–5 hours. He reported high early mortality of newly captured adults and noted the appearance of sores on the posterior mantle tip of long-lived squid. LaRoe placed window screening over the larger tanks to prevent squid from jumping out, and reported adverse reactions from rapid changes in illumination. Our results differ from his in experimental approach, and we suggest that future studies might wish to evaluate both the ultra-violet illumination and bottom substrates used by LaRoe.

Mikulich and Kozak (1971) reported survival times ranging from 23 to 35 days for the oegopsid squid, *Todardoes pacificus,* when held in large concrete tanks. They observed feeding on a variety of food items, and determined daily rations approximately one-quarter of the squid's weight.

The rearing studies carried out by von Boletzky, *et al.* (1971) and by Arnold, *et al.* (1972) dealt with small species (1–3 cm dorsal mantle length) which spend much of the daytime in sand substrates. Both reports list survivals of approximately 200 days with attainment of full sexual maturity. Spawning occurred in three species reared by von Boletzky, *et al.*, with subsequent death of females (in a few days) and males (in a few weeks). They attributed aquarium mortalities to starvation and skin diseases, noting that smaller animals succumb most readily. Arnold, *et al.*, reported cannibalism occurring when dissimilar sizes were placed in the same tank. Recurrent in these rearing studies is comment concerning difficulty in selecting and presenting food organisms and the tendency of squid to starve over a short period of time. Because of differences in size, we do not feel justification in direct comparisons with the above reports; Bidder (1950) reported rapid digestion in several larger species which is in a much shorter time scale than our observed mortalities. We caution against the transfer of maintenance techniques from one group of cephalopods to another without evaluation of individual requirements.

In concluding this study, we are tempted to generalize on experiences gained from studying the (relatively short) laboratory survival of nearly one thousand *L. pealei* (Summers and McMahon, 1970, 1974, and present report) and from communications with colleagues working on related projects. Progress in our own case can be measured from the results shown in Figure 3, which contrasts squid survival of our earliest and latest work. The exponential "decay" in survival experiments of 1969 has become a cumulative lognormal mortality in the latter half of 1971. Both mean and median survival times have been extended four-fold and it is now practical to speak of a reasonably lengthy survivorship. (Among the 120 squid in experiments four, seven and eight of 1971, 24% lived longer than

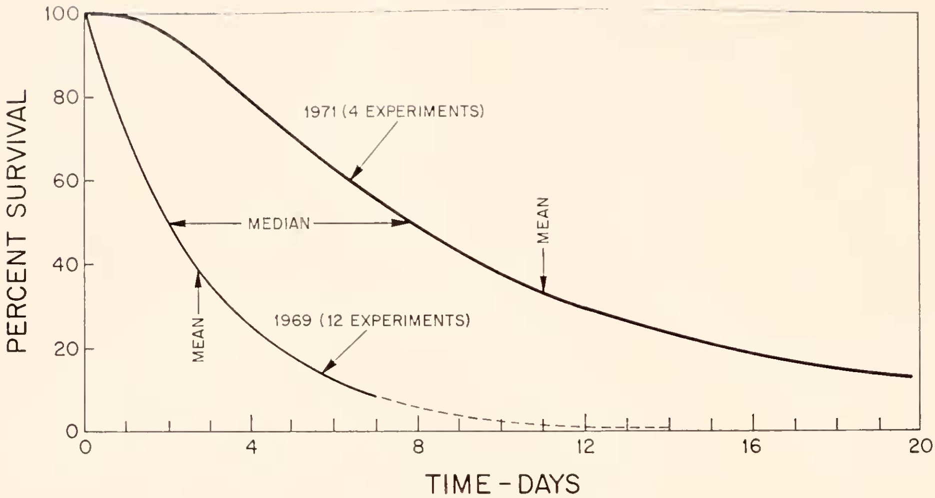

FIGURE 3. Survival models fit to the data from two groups of maintenance experiments. Experiments were truncated at one week in 1969, but the data from approximately 260 squid suggested a proportional mortality with a half-life of two days as shown. A lognormal mortality is indicated for 120 squid in the final experimental design employed in 1971 (the fifth experiment was not included; see text); this extended to 58 days, the record survival time. Improvements in maintenance techniques are apparent in the results both early in the experiments and through the course of the experiments.

two weeks, 12% lived longer than three weeks, 4% lived longer than four weeks, to the record survival of nearly two months.)

Improvements in our initial survivorships were probably due to modifications in the capture techniques. Much room for further improvement exists in this area, though practical considerations will probably always limit the methods employed. Ample water exchange, low disturbance, opaque tanks with lids and regulation in changes of illumination appear to be universally important for the maintenance of non-burrowing squids. Within natural limits, squid seem to tolerate a variety of seawater temperatures and crowding conditions and, feeding regimens. Mortalities resulting from collisions with the tank walls can be minimized by using larger tanks and/or applying bumpers inside the tank walls. Breeding and egg deposition are indicators of subsequent death, usually sooner in the case of females. The simple attainment of sexual maturity may augment mortality, as witnessed by several truncated rearing experiments (Choe, 1966; LaRoe, 1971; Arnold, *et. al.*, 1972). Thus, obtaining virgin individuals or sexual isolation may be of little value. Sorting for age groups (perhaps, simply by size) will probably aid in promoting survival. Rearing of species through complete life cycles will be most readily accomplished in those cases where the eggs are large and the fry are well developed (*L. pealei* does not possess these advantages). As stressed by LaRoe (1971), the selection of food types will be a problem in many cases.

The authors wish to acknowledge the considerable help given them by numerous colleagues and the staff of the Marine Biological Laboratory. Drs. H. Burr Steinbach and Edward F. MacNichol were especially instrumental in stimulating this project. Several friends and associates were made to perform hard physical work, log data and sort through trawl catches in exchange for day trips aboard the fishing vessels, most durable among whom was Ms. Eleanor Lipshitz. Other colleagues provided comments and suggestions on call and endured our obsession with squid. We especially wish to cite Captain Henry Klimm and the personnel of the National Marine Fisheries service in this respect. Captains Peter Graham and David Graham and their respective crews were very helpful in this project. Drs. John M. Arnold and David E. Schneider provided useful criticisms of both manuscripts.

Summary

1. This paper reports continued experimentation on factors affecting the survival of the squid, *Loligo pealei,* in laboratory aquaria. A total of 246 squid were studied in eight separate experiments which were run between May 18 and December 4, 1971.

2. Various tank sizes and configurations were studied in conjunction with evaluations of a tank wall bumper system and relative water temperature. Uncontrolled factors such as ambient seawater temperature, age, sex and sexual maturity were studied over the course of the experiments.

3. Mean survival of all squid was 177 hours and maximum survival was 1400 hours. In the final design, the mean survival was 248 hours (120 squid). Mortalities in this last group closely followed a log-normal model. The bumper system was found to produce significant survival advantage (with better than 99% confidence) through an analysis of variance of one experiment.

4. The "state of the art" is discussed with some generalizations and suggestions for further investigations.

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